

## Table of Contents

Abstract .....	1
Introduction and Purpose .....	2
Background .....	2
Location and Age of Deposits .....	4
Methods .....	6
Results: Composition of the Pollen Flora with Respect to the Megafossils .....	7
Ferns and Fern Allies .....	7
Gymnosperms .....	8
Monocotyledons .....	9
Dicotyledons .....	10
Magnoliidae .....	10
Hamamelidae .....	10
Caryophyllidae .....	12
Dilleniidae .....	13
Rosidae .....	13
Asteridae .....	15
Uncertains .....	16
Discussion .....	
Relation of the Leaf and Pollen Floras .....	16
Geographic Floral Elements and Ecological Conditions .....	18
Climatic Conditions Estimated from the Flora .....	20
Paleoaltitude of the Florissant Basin in the Context of Climate .....	22
Conclusions .....	24
Acknowledgements .....	25
References Cited .....	25

**COMPARISON OF FLORISSANT LEAF AND POLLEN FLORAS,  
CENTRAL COLORADO, AND CLIMATIC IMPLICATIONS**  
**with edits 3/24/97**

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**ABSTRACT**

The rich Florissant leaf flora dated at 34 .1 Ma, and identified by Harry D. MacGinitie's classic work, is well represented by the fossil pollen/spore flora. Pollen identifications from various parts of the Florissant Formation corroborate the generally warm temperate character of the flora indicated by fossil leaves and add a number of warm-temperate to subtropical taxa to the flora: *Cyclocarya*, *Engelhardtia/Alfaroa*, *Pterocarya*, (walnut family), *Fagus*, (beech) and *Eucommia*. These types are generally associated with a summer-moist climate in Eastern Asia or North and Central America. In addition, remains of a fossil palm leaf are reported here. Several taxa including greasewood (*Sarcobatus*,) and other saltbushes, indicate a seasonally dry climate, as described by MacGinitie. A few taxa (Onagraceae) suggest affinities with woody groups of Northern Mexico.

Twenty three of the 38 families of vascular plants identified from fossil leaves are corroborated by pollen and spores. Of the 84 genera of vascular plants MacGinitie described in the leaf flora, some 26 have been found in the microfossil record. The 23 genera added to the flora by microfossil evidence provide evidence of several new families, including Selaginellaceae, Schizaeaceae, Elaeagnaceae, Rhoipteleaceae, Ericaceae, Onagraceae, Chenopodiaceae, Eucommiaceae, and a member of the Fremontodendreae has verified the family Sterculiaceae. We report three new conifer genera.

The strongest corroboration of leaf taxa (about 85%) is with the wind-pollinated groups that are high pollen producers, while among those groups that are moderately low to low pollen producers including many insect-pollinated types, the representation of taxa by pollen is below 10%.

The diversity of this flora is indicated by the 112 species identified by leaves, while more than 150 phenotypes are found among the pollen and spores.

Samples from a measured section of the lower part of the Florissant Formation indicate that Taxodiaceae (TCT) pollen types are common (10-35% of the tally), Pinaceae are less common (5-25%), Ulmaceae types are from 5 to 15%, and Fagaceae and Juglandaceae pollen are more rare ranging from 1 to 10% of the total count. *Fagopsis*-type pollen reaches about 10% in occasional samples.

The evidence from the microfossils fits well with conclusions from fossil leaves and fruits, as well as from the fossil insects, that the climate was relatively equable and warm-

temperate, with mild winters. If the present lapse rates in Colorado are an indication, the flora suggests a relatively low elevation, probably below 1000 m (3000 ft) as suggested by MacGinitie for the Florissant interval and the Eocene/Oligocene transition. Though lapse rates may have been lower than now, conditions during the Eocene are probably not yet well enough known to estimate quantitatively the altitudes of mid-continent basins using this method.

**[VALID SEALEVEL MAT?]**

## **INTRODUCTION AND PURPOSE**

Much has been written recently about the environment and topography of the Florissant basin at the time the fossil-bearing sediments accumulated, but not all the evidence is in agreement. How and when did the basin get to its present elevation? One pertinent line of paleoclimatic evidence comes from the fossil plants. The present report on pollen and spore evidence is significant in two ways: one is because it adds new plant genera, of which several are warm temperate to sub-tropical in distribution, and the second is because our microspore identifications corroborate a number of taxa from the identified leaf flora.

The monograph by MacGinitie (1953) on the Florissant fossil leaves stands as a model of careful work which all contributors to this volume build upon. The care with which he studied the taxonomy and modern affinities of the flora becomes apparent when one notes how few assignments have been changed over these years since publication.

The pollen work reported here, which was begun by the first author while working at the U.S. Geological Survey in Denver CO, is designed to compare the fossil pollen and spore types with modern pollen and spores of the groups that MacGinitie identified at Florissant. How well do the pollen and spore types corroborate the megafossil identifications? What biases do we face in the pollen record? Do pollen grains provide the same ecological and climatic picture of the flora as the megafossils?

## **BACKGROUND**

The leaf flora of the Florissant Formation identified by MacGinitie includes some 114 species of plants, one of the largest leaf and fruit floras of Tertiary age in the western USA. Manchester's taxonomic review (this volume) of the megafossils shows number of Florissant taxa to be still around 110-120. The chief families represented by leaves are the legumes (9 genera), the rose family (7 genera), and the Sapindaceae (6 genera). The pollen flora that we can identify is more limited and shows a different spread of taxa, especially of gymnosperms, and dicotyledonous groups known to be large pollen producers.

MacGinitie determined that the nearest modern analogue of the flora is in the subhumid mixed deciduous and conifer vegetation of northeastern Mexico, where the average annual

temperature was no less than 18°C. One such analogue area is in the highlands of Tamaulipas Province in Northeastern Mexico (N. Lat. 23°) described by Martin (1958). At an elevation of about 1800-2800 m (4600-7600 ft) there exists an evergreen oak/pine association (Leopold, 1950; Puig, 1976) which may have been similar to that in the late Eocene highland areas around Lake Florissant. At about 800-1500 m (2500-4500 ft) on the Tamaulipas slopes is a rich deciduous (caducifolicee humid de montagne; Puig, 1976) hardwood forest with a few conifers that includes a wide array of genera such as may have grown around the low areas near the Lake Florissant. Some of the hardwoods are closely related to riparian species that occur in lowland environments of the Edwards Plateau of central Texas (MacGinitie, 1953). On the dry eastern side of the Sierra Madre Oriental stands a dry forest dotted with pines and evergreen oaks. The oaks grow stunted and gnarled with spreading crowns, usually less than 80 feet tall. The vegetation is more sparsely distributed than in the cloud forest, and may be a good analogue of the highland vegetation above the Florissant basin.

The fossil vegetation recorded at Florissant (MacGinitie, 1953) is chiefly woody, warm temperate and more diverse in summer-moist forms than is the present flora of Florissant, Colorado, which contains an abundance of herbs and sub-arid shrubs of the *Pinus ponderosa* woodland (Edwards and Weber, 1990). While the present climate of Florissant is summer-dry and cool temperate with heavy freezing in winter, (Mean Annual Temperature [MAT] = 4°C; **range = \_\_\_\_°C; mean annual precipitation is \_\_\_\_ cm; Nat. Park Service records**), the general climate of the region cited by MacGinitie, the Sierra Madre Oriental piedmont region down to 22°N Lat., has an MAT of >18°C, a range of monthly mean temperature of 10-13°C and a precipitation of below 600 cm/year (Koeppen, 1948; Puig, 1976). Below 1800 m the climate is fairly frost-free.

In the Florissant basin, ponderosa pine (*Pinus ponderosa*) woodland with some lodgepole pine (*P. contorta*) extends down to ca 2700 m (8000 ft) and does not grow on the lake deposits in the center of the basin. Colorado blue spruce (*Picea pungens*) occurs where the granite bedrock is close to the surface and with Douglas fir (*Pseudotsuga menziesii*) occurs in the draws and cool stream valleys. Engelmann spruce (*Picea engelmannii*) becomes dominant above 3300 m (10,000 ft), and altitudinal tree line is at ca 3800 m (11,300 ft). The modern pollen rain at Florissant is overwhelmingly dominated by pine, with sage (*Artemisia*), grass and pollen of other herbs represented.

Previous work on Florissant Formation sediments includes the study of laminae by McLeroy and Anderson (1966) by which they estimated the length of time that might have been involved for the deposition of the lake deposits. Early identifications by Leopold (1965) and her photographs of Florissant pollen furnished for Penny appeared in Tschudy and Scott (1969) and established some of the key taxa. A comprehensive survey with pollen counts by Hascall (1988)

documented pollen and spores from the section that Taggart and Cross describe (this volume). A trend during the Eocene showed a decline of Old World tropical taxa and their replacement by New World tropical types in the Rocky Mountains (Leopold and MacGinitie, 1972); Florissant is a benchmark flora in that it comes at the end of the tropical period of the Eocene. Our pollen diagram from the lower part of the Formation shows relatively little vegetative change (Leopold, Liu & Clay-Poole, 1992).

## LOCATION AND AGE OF DEPOSITS

A number of field studies indicate that the topography of the Florissant basin was similar to that which we see today (Epis and Chapin, 1968, 1975). The extent of the Florissant Formation outcrops, based on walking the margin of the outcrops (Wobus and Epis, 1978; Leopold and Lind, unpublished report for the Nat. Park Service, 1964), seems generally to be delineated by the treeless area on topographic maps (Lake George Quadrangle, USGS, 1956, 1:24000). The isotopic age of the Florissant Formation, 34 million years (Ma), was originally established from K/Ar dating on volcanoclastic flow rocks that overlie the lake sediments (see Evanoff, this volume; Epis and Chapin, 1975). Newer evidence from Ar<sup>40</sup>/Ar<sup>39</sup> dating shows that the Florissant Formation is bracketed by an age of 33 Ma on the overlying volcanics and 36.6 Ma from the underlying Wall Mountain Tuff; based on the association of Chadronian mammals and using the Eocene/Oligocene boundary age, the formation is late Eocene (Evanoff, 1994; 1992).

The sites from which sediment samples were prepared for fossil pollen come from areas in the north and central parts of the Florissant Basin, as indicated in **Figure 1** (map). The first sediments prepared, D1095 and D1083, were from hand samples received from other workers, and the locality information for these is lacking. The long section (13 meters, see Appendix) is University of Washington paleobotanical locality **W1** from the road cut 1/2 km east of the Florissant townsite (Photograph in **Fig. 2**). In the list of localities below, arranged from older to younger sites, the D numbers refer to U.S. Geological Survey Paleobotanical Localities.

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Figure 1 Map of the Florissant Basin near here.

Figure 2. Photograph of road cut near here.

### -----NEW TABLE -----

- D1177** Road Cut East of Stoll's Ranch.. NE1/4 SW1/4 NE1/4 Sec 3 T13S R71W. Leopold measured section: grey concoidally fracturing clay beds overlie laminated leaf-bearing shales. This is also Cockerell's locality 7b (1909), and it lies at the north end of the Florissant basin.
- W1** Road Cut on south side of Hiway 24 (photograph looking south, **Fig. 2**) just east of townsite. See field sketch, W1/2 NW1/4 SW1/4 Sec. 1 T13S R70W, 8200 ft. elev. Leopold coll. and measured section, remeasured by Emmett Evanoff, 13 meters exposed. These are the "Amyzon" fish beds of Cope (1875) on the north end of the Florissant basin. It records an arkosic unit at the base (Unit 2) abruptly overlain by mudstones, pumicious sands and clay, with laminated silty clay and pumice to the top of the section.

- D1197** Florissant Formation from trench behind the former Singer Ranch buildings, elevation 8400 ft. Includes 9 samples from top down, covering 17 feet of section. SW1/4 Sec 13 R71W T13S. Unit Tf2?.
- D1496** MacGinitie's "Fish Bed Locality" Field loc. EL58-43A thru -E plus leaf impressions, ca. 8440 ft elev.; Center W1/2 SE1/4 NE1/4 Sec 24, R71W T13S. Leopold and MacGinitie collections. Site is about 1/8 mile north of buried aqueduct line that crosses west to east.
- D3495** At Snare Ranch- one sample. 9/1964. 500 ft NW of gate to Nat Snare Ranch Elev. 8525 ft. Sec. 25, R71W T13S.
- D3496** Behind School House, Florissant Grange Building at base of Crystal Peak Road E1/2 NW1/4 SE1/4 Sec. 2, R71W, T13S.
- D5464** South side of Twin Rock Road at 8600 ft elev. SE 1/4 SW 1/4 Sec 19 T13 S, **R70W?** Leopold and Carol Lind coll.
- D1175.** Elso Barghoorn and Richard Scott's collections at Roland W. Brown's site. Samples A and B. NE1/4 SW1/4 NE 1/4 Sec 3, T13S, R71W Lake George. 3/19/56.
- Uncertain:
- D1095** F.S. MacNeil sample; undetermined locality, Florissant.
- D1083** Roland W. Brown sample, US Nat. Museum Loc. No. 9327. specimens 50323 and 50343.
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The samples we used were those we collected chiefly from lacustrine sediments, many being laminated paper shales with graded bedding (fining upward) suggesting sequential ash falls. Laminae range from about 2 mm to 9 cm in thickness, the lower parts of each lamina were typically of silt or fine sand-sized particles, grading upward into silt with clay-sized sediments. At one section (D1177) we sampled a thick massive silt and clay bed that contained abundant algae and occasional pollen. Evanoff has remeasured our section **W1** in detail in 1993 and has kindly made it available to us here (see Appendix); the thickness of the lithologic units and the position of our pollen samples are shown in **Fig. 3**. Based on field examination of D1177 and **W1** sections with Emmet Evanoff and others in August 1994, Evanoff has stated (personal communication, August, 1994) that these northern localities represent the lowermost parts of the Florissant Formation.

## METHODS

The photomicrographs and taxonomic research were primarily by the first author, and the counting of pollen and spores for the pollen diagram was shared by both authors. Identifications were based on modern pollen reference slides that cover a wide number of taxa from East Asian and New World tropics and temperate zone, collections that are housed at the US Geological Survey Paleontology and Stratigraphy Branch in Denver and at the Pollen & Seed Laboratory, Department of Botany, University of Washington, Seattle.

Preparation methods followed Doher (1980), starting with careful cleaning of fresh sediment blocks, crushing with mortar and pestle to pea-sized chunks, and initial treatment with 10% HCl to dissolve carbonates which were occasionally present. Hydrofluoric acid treatment was from several hours to overnight at room temperature. Acetylation of sediments was followed

by swirling and panning treatment to clean up the residue. Fossil pollen were mounted in glycerine jelly with safranin O as a light stain. Cover slips were sealed with plastic. Slides and extra samples will be stored at the US Geological Survey Paleontology and Stratigraphy Branch laboratory in Denver.

Counts of fossil pollen included from 200 to 500 grains per slide.

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Figure 3 Measured section

Figure 4 Pollen Diagram Near here

Table 1 List of identifications

Table 2 Comparison of leaf, fruit identifications with the pollen flora

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## RESULTS: COMPOSITION OF THE POLLEN FLORA WITH RESPECT TO THE MEGAFOSSILS

The plant taxa identified from spores and pollen (**Table 1**) are shown with their taxonomic relationship with the megafossil record in **Table 2**. The spore data add at least two fern allies to the flora, and pollen of gymnosperms indicate the presence of at least three additional genera of Pinaceae. Pollen of angiosperms provide evidence of one additional monocot, and add seven genera of Hamamelids, one genus of Caryophyllidae, nine Rosidae generic types. Of the 84 identified leaf genera, about 40 are so far found from microfossil evidence and 23 generic types are new. Of the 43 families identified from vascular plants, some 21 are corroborated by pollen and spore evidence, or by phenotypes that may represent the family types. Algal types that are locally abundant such as *Pediastrum* and *Botryococcus* are described by other authors (Nichols et al.; Cross and Taggart, this volume).

Relative numbers of pollen and spores in the tally for section **W1** are plotted on the pollen diagram (**Fig. 4**)

### Ferns and Fern Allies

Among the spores of vascular plants, *Selaginella* is represented by several spore types. One is an excellent match for the spores of *Selaginella densa*, (Plate 1 Figs. 2, 3) an herbaceous ground-cover plant that is common on dry exposures in the Rocky Mountains. Trilete spores of this type with a flange along the equatorial plane are also commonly seen in Miocene deposits of the western North America. Several other types are *Selaginella* cf. *S. longipila* (Plate 1, Fig. 1) cf. *S. sanguinolenta* (Plate 1, Fig. 4) and cf. *S. mairei* (Plate 1, Figs. 5, 6). Though the genus is cosmopolitan, the resemblance to *Selaginella* species is striking.

A large smooth trilete spore (Plate 1, Fig. 10) with thick walls looks very much like the large spores we extracted from a leaf fossil of *Lygodium kaulfussii* (Schizaeaceae), a species that is common in other Eocene deposits in the Rocky Mountain region (Leopold p. 53 and Plate 36 Fig. 10 in MacGinitie, 1974). We report similar Eocene spores in Love *et al.*, 1978. In situ spores are illustrated by Manchester and Zavada, 1987). The living genus has 25 species that are tropical and subtropical, though one species ranges northward along the eastern seaboard of the U.S. Genera of the family Schizaeaceae are primarily tropical taxa.

Several monolete spore types suggest the family Polypodiaceae.

## Gymnosperms

We found pollen representation for 3 of the 5 gymnosperm families, and 6 of the 7 megafossil genera, and have added several genera. MacGinitie compared the seeds of fossil *Abies* or true fir with *A. venusta*, (now *A. bracteata*), the Santa Lucia fir that is endemic to the mountains east of Los Angeles, CA. The *Abies* pollen we find is a large type 140 to 180  $\mu\text{m}$  in length (Plate 3, Fig. 2; Plate 4, Fig. 1) that compares very well with pollen of *A. bracteata* which is a unique type being the sole member of the most primitive section of the genus *Abies* (Liu, 1971). MacGinitie called the megafossil *A. longirostris* Knowlton.

*Picea* pollen (Plate 2, Figs. 1, 2; Plate 3, Fig. 1; up to 400  $\mu\text{m}$  in length) is hard to assign to a subgenus but generally resembles *P. engelmanni*. and/or *P. pungens*. (Engelmann spruce and Colorado blue spruce). MacGinitie had identified two species of spruce from seeds, one of which he compared with *P. noveitchii* Masters of the mountains of China and Japan. A Sierra Madre species, *P. chihuahuana* is like *P. Breweriana* of the Pacific Northwest, which also resembles the Florissant pollen type.

*Pinus* pollen in these sediments may represent several species, but because of the difficulty in separating even subgenera of pine, we can only cite a small type (Plate 2, Fig. 4) and a large type (Plate 2, Fig. 3; Plate 5, Fig. 2; aperture details are not preserved). The latter may be similar to *Pinus ponderosa* (see Hansen and Cushing, 1973), as MacGinitie compared *Pinus florissanti* to that species.

To the Pinaceae we have added *Cedrus* type (Plate 5, Fig. 1) based on the thick, smooth cappus, *Pseudotsuga/Larix* (Plate 4, Fig. 2) and *Tsuga* spp. (Plate 1, Figs. 7,8). All of these pollen types are uncommon at Florissant. Though the genus *Tsuga* is known from the middle Eocene (pollen records in Wodehouse, 1933; Leopold and MacGinitie, 1972; winged seeds in Wehr and Schorn, 1992), *Pseudotsuga* and/or *Larix* represent an early occurrence in the western USA, and are not yet recorded in earlier sediments elsewhere (Hermann, 1985). *Cedrus* pollen types are occasional in Miocene sediments in Alaska (Leopold and Liu, 1994) and was widespread in Oregon (Gray, 1964, p. 29).



From a hand fossil of *Sequoia affinis*, Leopold removed a male cone and obtained thousands of Taxodiaceae pollen grains. We find that a few of these are characterized by a small papilla about 5  $\mu\text{m}$  in length, but most have no papilla at all, in contrast with the pollen of extant *Sequoia* in which most grains are papillate. The gemmate surface sculpture is similar to that of *Sequoia* and *Sequoiadendron*. It may be difficult to discern the papillate grains from pollen of *Torreya*, or the non-papillate grains from *Chamaecyparis*, both having been reported by MacGinitie. In our counts we lump all the Taxodiaceae, Taxaceae and Cupressaceae into one group ("TCT", Plate 4 figure 3), and these grains comprise up to 30% of the count.

We are able to corroborate one other important gymnosperm found by MacGinitie, *Ephedra*, thought to be related to *E. nevadensis*. Pollen of the *Ephedra* cf. *E. nevadensis* type (Plate 4, Fig. 4) appears in almost every sample. We also find *E. torreyana*-type pollen (not figured; Steeves and Barghoorn, 1959 ) regularly here. *Ephedra* pollen comprises 2-6% of the count and is always present in Florissant samples.

### **Monocotyledons**

A palm leaf fossil found by Estella Leopold and students near locality D1496 (*Palmites*; figured by Manchester this volume) is an important addition to the flora. Though Lesquereux (1874) had assigned two fruits to *Palmocarpon*, Knowlton (1916) doubted these could be palms, and commented that the family was unknown at Florissant. Our palm leaf which has been identified by MacGinitie (personal communication, 1975) and by Manchester (this volume), changes that fact. Undoubtedly some of the smooth monosulcate pollen may represent this group or other monocots (not figured).

Pollen of the grass family (Gramineae; Plate 8, Figs. 1, 2) is occasional and rare at Florissant. The sediments have also yielded excellent macrofossils which MacGinitie identified (from a single fruiting body) as "*Stipa*". This is one of the earliest known identified grass macrofossils according to Thomasson (1980), important because it represents an extinct Stipae, a subfamily that became common and dominant during the Miocene in deposits of the Great Plains (Elias, 1942; Thomasson, 1986). Agnes Chase once identified well preserved Florissant fruits related to *Muhlenbergia* (Knowlton, 1916, p. 250). Grass pollen appears occasionally in Eocene and Oligocene deposits in western USA (Leopold and Denton, 1987; Leopold, Liu, & Clay-Poole, 1992).

Though not abundant, monoporate pollen representing the Typhaceae (cattail; *Typha* cf. *T. angustifolia*, Plate 8, Fig. 3), suggests lakeside aquatics. MacGinitie found both narrow and wide-leaved cattails in the flora, and leaf and fruit remains of another aquatic *Potamogeton* are figured by Manchester (this volume).

A lily or amaryllis type (Plate 5, Fig. 3) is rare. We did not find pollen of the *Smilax* type, a monocot identified by MacGinitie. Water lily of the Nymphaeaceae, *Nuphar* type, is an addition to the flora, though not a common pollen type (locality **W1**).

## **Dicotyledons**

***Magnoliidae.*** The diverse laurels in the leaf record are not apparent in our pollen assemblage, probably because their pollen is poorly preserved in sediments. A few pollen grains of *Berberis* suggests the identified *Mahonia* (now called *Berberis*; Oregon grape) leaf type.

***Hamamelidae.*** The subclass Hamamelidae or witchhazel group which is chiefly wind-pollinated, is especially well represented in the pollen record. We add new families (Rhoipteleaceae, Eucommiaceae), and many new genera for families that are already known here: Betulaceae, Juglandaceae, and Ulmaceae. One megafossil of the Hamamelid family (Platanaceae) has a possible counterpart in the pollen record (cf. *Platanus*), that looks very similar to *Platanoidites* pollen from earlier Eocene sites (Leopold in MacGinitie, 1974, **Plate \_ Fig. \_**).

In the Juglandaceae (walnut family) leaves and fruits of *Carya* have been reported (MacGinitie 1953, p. 96), and a locule cast of *Juglans*, black walnut type, is identified by Manchester (1987). Leopold reported Juglandaceae pollen in Penny, (**1972; Plate \_ Fig. \_**). Pollen of this family includes not only *Carya* (hickory) and *Juglans* (walnut), but also *Pterocarya* (ling nut), an Asian warm-temperate group, and *Engelhardtia/Alfaroa*, which are tropical and subtropical genera, the former having 5 species in Southeast Asia and the later with 3 species in Central America, comprising the group Engelhardtiae (Nichols, 1973). The American taxa have somewhat larger pollen than the existing East Asian species, and the Florissant fossil may be related to *Alfaroa*. We also report *Platycarya* (Plate 8, Fig. 9), a monotypic genus found chiefly in the Mixed Mesophytic forest in Southeastern China (Wang, 1961; Wing and Hickey, 1984). The genus is usually restricted to lower and middle Eocene strata in the Rocky Mountains (Leopold and MacGinitie, 1972). In addition to these a most unusual member of the walnut family is *Cyclocarya*, the pollen of which is quite characteristic as a minor element of the Florissant flora (Plate 8, Fig. 13, 14). While *Carya* is the most abundant of these and represents from 10-25% of the tally, *Juglans* and *Pterocarya* are in every pollen sample in amounts around 1-3%, and *Cyclocarya* and *Engelhardtia/Alfaroa* are in a few samples as trace elements (ca. 1%). *Engelhardtia* had been reported but not figured by Lesquereux (1874).

A first in the Eocene/Oligocene pollen record may be the monotypic family Rhoipteliaceae, another member of the Southeast Asian subtropics and warm-temperate summer-moist forest. Pollen tentatively assigned to that family (Plate 8, Figs. 7, 8, 10, 11, 12) shows strong arcs between the apertures, and its pores are simple and oblong. The wall has a thick

ektexine with a tectum ("tegillate") and the sculpture is faintly microreticulate. Plate 5, Figs. 12, 13, 14 may also be Rhoipteliaceae-type pollen, though the grain does not present a true polar view. Rhoipteliaceae reaches 6-8% of the pollen tally in section W-1 and it appears in about half of our samples. Wolfe (1973) has reported *Rhoiptelea* pollen from the Upper Cretaceous sediments of Eastern USA.

The Betulaceae (birch family) is represented in the Florissant leaves of the *Carpinus* (hornbeam) type assigned to an extinct genus *Asterocarpinus* (Manchester and Crane, 1987; Manchester, this volume), but the pollen seems to be consistently 3-pored and of the *Ostrya*-type which includes *Carpinus* (Plate 8 Fig. 5). Affinity with *Carpinus* which has 3-4 pored pollen cannot be excluded. *Ostrya-Carpinus* pollen reaches 5% near the top and base of section W1.

An important group is the Fagaceae (beech family), especially the extinct genus, *Fagopsis*, (Manchester and Crane, 1983), the most abundant leaf fossil at several localities that are presumed to be shoreline facies (MacGinitie 1953). Pollen of *Fagopsis* which Leopold extracted from flowering male aments yielded hundreds of tricolpate smooth pollen with indistinct "pores", similar to the type shown in Plate 6 Fig. 7. Fossil leaves of *Quercus* (oak) are diverse (about 9 spp. that MacGinitie said are hard to distinguish), and they all seem to represent evergreen oaks. Among the oak-type pollen we found, one is assigned to *Quercus* as it is tricolpate with furrows bent at the equator, and scabrate sculpture as in many deciduous oaks today (Plate 5 Fig. 6; Jarvis et al., 1992). A second is a mystery-type with a longer polar axis, tricolpate with inrolled margins and scabrate sculpture (Plate 5, Fig. 7). Almost everything about the latter suggests *Quercus*, but we know of no modern Quercoid or Fagaceous species whose pollen has such a long polar axis. Crepet (1989) has described a number of extinct genera in the Fagaceae of Oligocene and Eocene age, and this may well be a Fagaceous pollen type. In addition to these, we have recorded several grains of *Castanea/Castanopsis* (not figured), which clearly support MacGinitie's determination of *Castanea* (chestnut) leaves, though Manchester did not find the leaves convincing. We have figured pollen of *Fagus* (beech; Plate 6, Figs. 10, 11), a new member of the flora. Quercoid pollen reaches 20% of the pollen count and is present in every sample, while *Castanea* type and *Fagus* are rare.

In the Ulmaceae (elm family) pollen of Ulmoidae include abundant 3, 4, and 5-pored elm types. Though at one time we assumed the predominantly 4-pored pollen of *Zelkova* (Asian elm) may have been present, Manchester (1989; 1987) indicates that the abundant "*Zelkova*" leaves are probably an extinct type "*Cedrelospermum*". His decision is based on the attached fruits. Fossulate, predominantly 5-pored *Ulmus*-type pollen is common, especially in the lower part of section W1. At Florissant, we have occasionally seen 6-pored pollen that has low verrucae and thickened pore areas, reminiscent of *Hemiptelia*, an Asian genus that Elizabeth Wheeler (this volume) has reported from wood remains. Ulmoidae pollen represents up to 35% of the tally.

The family Eucommiaceae, with its monotypic genus *Eucommia*, is another new addition to the flora. *Eucommia* is a deciduous warm-temperate tree of SE Asia. Its pollen (Plate 5, Fig. 5) is smooth, tricolpate with infolded furrows and orate apertures at the equator. *Eucommia* is a regular member of the middle Eocene forests in the Rocky Mountain region (Leopold and MacGinitie, 1972; MacGinitie 1974), and at Florissant its pollen is an occasional but consistent element. It endured much longer in Western Europe (Pliocene) than in Western North America.

Leaves of *Morus* (mulberry, Moraceae) and rare two-pored pollen of the *Morus* type (not figured) were found, though Manchester (this volume) rejected the leaf identification.

**Caryophyllidae.** The subclass Caryophyllidae, which does not appear in the leaf record here, has at least two families represented by their pollen. Chenopodiaceae (salt bush family) or *Amaranthus*-type is common or present in every sample. Most of the Chenopodiaceae grains appear identical to *Sarcobatus* (greasewood; Plate 9, Figs. 11-14), which today ranges from the Great Basin southward to Mexico, and is a common pollen type throughout the Rocky Mountain Eocene. Other grains (Plate 9, Fig. 15) may represent either Chenopodiaceae or *Amaranthus*-type. Another member of this subclass is a pollen grain of Caryophyllaceae (chickweed family; not figured) and resembles *Silene* or *Stellaria*. If in place (if not a contaminant) this is an early record for Caryophyllaceae, which generally is not known at mid and high latitudes before the Miocene (Leopold and Denton, 1987; Leopold and Liu, 1994).

**Dilleniidae.** Of the four Dilleniid families, the pollen evidence corroborates two, the Salicaceae (willow family; *Populus*, *Salix*, not figured) and the Sterculiaceae. We have no evidence of Styracaceae (*Halesia*) and no certain records of Tiliaceae (*Tilia*), though the Sterculiaceae pollen "*Fremontia* type" (Plate 6, Fig. 15) looks similar to *Tilia*, except that it lacks strong thickenings under (around) the pore. In this feature it does not fit with Bombacaceae pollen types. Manchester (1992) has also found similar pollen taken from the flowers of an extinct genus, *Florissantia*, which he placed tentatively in the Sterculiaceae. Our fossil pollen closely resembles the pollen Manchester extracted from *Florissantia* flowers. This pollen type strongly resembles the section Fremontodendreae of the Sterculiaceae, and supports Manchester's family assignment. Similar small sterculiaceae grains are typical in middle Eocene floras of the Rocky Mountains (Leopold in MacGinitie, 1974, Plate 44, Figs. 14, 16, 17, 18).

**Rosidae.** Although by far the greatest megafossil representation of plant families is in this group, pollen representation is poor. Of the 43 rosid genera only 6 have been found using microfossil evidence. Four new genera including 3 new families are found in the pollen record.

Identified pollen of the rose family includes *Malus* (apple; Plate 5 Fig. 11) and/or *Pyrus*, which is similar. *Malus* is first recorded from megafossils in the middle Eocene at Republic (Wehr and Hopkins, 1994), a montane site in Washington where Wolfe and Wehr (1987) described an early diversification of this family. Leaf evidence of 7 rosaceous genera including *Rosa* and *Malus* clearly indicates the importance of this family at Florissant.

*Acer* (maple; Plate 5, Fig. 8-10) pollen is reminiscent of *Acer glabrum* and supports the record of *Acer* leaves and fruits. The fossil pollen is distinct from *Dipteronia* in the maple family.

With its syncolpate breviauxial features and reticulate sculpture *Cardiospermum* pollen (Sapindaceae) is unmistakable (Plate 7 Figs.3-7). *Cardiospermum* is an herbaceous or woody vine in warm temperate areas from Missouri into Mexico and in the West Indies. The species this pollen most closely resembles is *C. halicacabum*, which inhabits tropical Mexico. This is the same species that the leaves of *Cardiospermum* resemble. Pollen of *Dodonaea*-type is present (Plate 7, Fig. 1; leaves of *Dodonaea* occur in the flora), and one other sapindaceous pollen (trisyncolpate reminiscent of *Cupanaea*) is found at Florissant. (Sapindaceae pollen were reviewed in some detail by Muller and Leenhouts, 1976).

In the Vitaceae (grape family) , *Parthenocissus* (five-finger vine) or possibly *Cissus*-type pollen are occasional in our counts (not figured). *Parthenocissus* is a hardy, adaptable vine common in damp woods. In western US it ranges southward from the Rocky Mountains into Mexico and Cuba.

*Croton* in the Euphorbiaceae (Plate 9, Fig. 5) is represented in the pollen record by a few specimens. *Croton* is an important member of the Tropical Deciduous Forest and Thorn Forest in Northeastern Mexico (Martin, 1958).

*Ptelea* (not figured; Rutaceae) is a rare pollen type; the genus is widespread in the USA and in Northeastern Mexico, and the living species MacGinitie has cited grows on rocky slopes or open areas along streams. Fruits MacGinitie assigned to *Ptelea* have been reassigned to Caprifoliaceae, *Dipelta*-like, though Manchester (this volume) reports two new *Ptelea* fruits and the trifoliate leaves.

In the Meliaceae both MacGinitie and Manchester have described *Cedrela* or *Toona* seeds, but we have not yet found pollen of this family at Florissant, though *Melia* pollen occurs in other mid-Tertiary floras of the region.

The following records indicate families or genera of Rosidae new to the flora:

Ericales: pollen represents an unknown taxon clearly a member of the Ericaceae or Pyrolaceae; it is figured in Plate 7 Figure 8.

*Petalostemon* pollen (not figured; Leguminosae) is an occasional form; the genus is a common perennial herb in the prairie flora of the Black Hills and eastern Great Plains.

Elaeagnaceae, *Elaeagnus* cf. *E. argentea* (buffalo berry) or cf. *E. communtata* (wolf-willow), are shrubs that have ecologically similar species in central and eastern China, and western USA. They inhabit open vegetation along water courses on both continents. This is a new family for Florissant, and its pollen is a regular minor element appearing in many samples. The *Elaeagnus* pollen type is recorded in Miocene of Oregon (Gray, 1964, Plate IV, Fig. 4), as well as at several Eocene localities (Leopold in MacGinitie, 1974, Plate 42 Fig. 28).

Onagraceae (evening primrose family). Two pollen types appear as rare elements at Florissant; one is *Semeiandra* cf. *S. grandiflora* (Plate 6 Fig. 3) a woody genus from the eastern Sierra Madre of Mexico, and the other is related to *Xylonagra* (Plate 6, Fig. 4), a shrub of Baja California. Each of these genera stand out as unique pollen types within the living Onagraceae. As far as we know these are the earliest records of the evening primrose family in the New World. It may be significant that these early forms are woody in habit. Recently Manchester (this volume) has found an Onagraceous flower at Florissant.

**Asteridae.** In the pollen record of the Asteridae we found three genera and three families new to Florissant. The new families are:

(1) Solanaceae. The pollen we identify as *Datura*, cf. *D. discolor* type, is striate with several pores (not figured). *Datura discolor* grows in subarid areas of Arizona and northern Mexico, and the genus *Datura* is warm temperate and subtropical in distribution (Avery et al., 1959).

(2) Apocynaceae cf. *Tabernaemontana*, *T. coronaria* type. This unusual tricolporate type has large pores thickened along their rims and with short furrows. Its wall has psilate to scabrate sculpture. Another probable Apocynaceae type is cf. *Trachelospermum* or *Parsonia* (Plate 9, Figs. 4, 6). This fossil type is a minor element in a wide number of Eocene floras, especially of Kisinger age (middle Eocene; Love et al., 1978, Plate 3, Figs. 7, 8).

(3) Malvaceae (mallow family; not figured). The pollen is malvaceous, large, multiporate with large spines, but the genus is unknown. Fossil mallow pollen represents a new record of the family at Florissant.

Of the four Asteridae families so far recorded by megafossils we have ascertained pollen types for two;

Caprifoliaceae. A new Florissant genus is *Viburnum* cf. *V. lentago* (Plate 6, Fig. 14). This pollen type regularly appears in the latest Eocene and Oligocene (White River Group) of the Rocky Mountain region. The pollen does not resemble *Sambucus* of this family, which is in the leaf and pollen record here. The outstanding sculptural feature is the graded reticulum which is

very coarse in the intercolpal equatorial regions, and is special in that this reticulum sometimes is deciduous, for we have seen many fossil specimens in which the sculpture is a deciduous net that peels off of the endexine.

Oleaceae. We have found *Fraxinus* -type pollen (ash), which is not similar to pollen of *Osmanthus*, a genus that was identified in the leaf flora.

### ***Uncertain***

Haloragidaceae, *Myriophyllum* type. We have a few good specimens of this and think it is a part of the aquatic flora of the lake. Similar forms are figured by Leopold and Liu (1994, Plate 2, Fig. 9).

Compositae. Pollen of this family include long- and short-spined types that are extremely rare. Only a few grains (< 5) have been seen among all our collections. These may not be fossils as we believe they are contaminants (see discussion below).

## **DISCUSSION**

### **Relation of the leaf and pollen floras**

Our identifications from pollen and spores (Table 1) provide new information concerning the composition and character of the Florissant flora. Within the leaf flora of about 100 species of vascular plants, some 62 are now of known geographic affinity. Of these 23 genera have been found in the microfossil record. The 21 new genera added to the flora by fossil pollen/spore evidence include about 4 subtropical types and 5 warm temperate to subtropical taxa. Some of these taxa have endemic distributions today in southwestern USA and/or SE Asia. Several (14) new families/groups have been added to the flora: Apocynaceae, Chenopodiaceae, Caryophyllaceae?, Ericaceae/Pyrolaceae, Elaeagnaceae, Eucommiaceae, Malvaceae, Nymphaeaceae, Onagraceae, Palmae, Rhoipteleaceae, Schizaeaceae, Selaginellaceae, and Solanaceae.

Of special interest are the occasional grains of Compositae, which if they are stratigraphically in place, would suggest the early occurrence of this highly advanced family. However, the grains we have found are either brightly stained or are stained differently, indicating they are modern contaminants that absorb somewhat more stain than the fossils; a few have evidence of protoplasm and cell contents that would be expected in fresh pollen, denying these as fossils. Further, the Eocene types we have seen, *Artemisia*, and long- and short-spined Compositae, are known in the literature to occur commonly as lab contaminants (e.g. MacGinitie, 1974, Plate 42, Fig. 22). The record of a single Caryophyllaceae? pollen, even though it looks like a fossil, because of its rarity is also in doubt, as most occurrences of this group are of Miocene or younger age (Leopold and Denton, 1987).

Groups within the leaf flora that are wind pollinated, and that are high-pollen producers, are most likely to be represented by the pollen flora as well. If we divide the identified leaf groups according to those that are (1) high producers of pollen or spores, (e.g. Juglandaceae, Chenopodiaceae, Pinaceae), (2) moderate producers of pollen (Aceraceae, Sterculiaceae, Salicaceae), or (3) taxa that are chiefly insect-pollinated and are low-pollen producers (e.g. Onagraceae, Berberidaceae, Moraceae, Rosaceae), we can measure the bias in favor of wind pollination in the microfossil record (**Fig. 5**). Within each category the megafossil taxa identified by MacGinitie and Manchester (solid bars) are corroborated by pollen evidence (cross-hatched bars) most strongly by the wind-pollinated plants that are high-producers (86%), compared to the moderate producers (27%) or the low producers (27%). For the new taxa added to the flora by microfossil evidence (polka dot pattern), we have found more new taxa from the first group (wind-pollinated: 12 taxa), than from the second (6) or the third (4) group. The ratio of all the pollen/spore types found versus all the leaf taxa among the high-pollen producers is 3:2, compared to the intermediate group (3:7) or the low producers (7:11). Thus we have a measure of the taxonomic representation according to pollen production that is obvious in the Cenozoic pollen record; the bias favors high-pollen producers and wind-pollinated plants (Fig. 5).

**Figure 5: Histogram of high, medium and low-pollen producers near here**

**Table 3 List of living taxa most like the fossil types, and their geographic groupings**

A high numerical representation of pollen in the tallies indicates a local abundance of Ulmoidae (reaching to 35%), *Carya* (to 24%), TCT or Taxodiaceae types (to ~35%) which probably combines *Chamaecyparis* (white cedar) and the more distinctive *Sequoia* pollen. From the abundance of their megafossils, these are considered to be riparian taxa growing near the lake. All these groups are high-pollen producers. The numerically abundant leaves of *Fagopsis*, the extinct beech type which MacGinitie thought was also a lakeside plant, is only moderately abundant in the pollen record; perhaps like certain other members of the beech family (such as *Fagus*), it was not a high-pollen producer; other megafossils in the same category include cf. *Typha* (cattail) and *Populus* (poplar). Subarid scrub types, *Sarcobatus* and related saltbush Chenopodiaceae and *Ephedra* are regular minor elements in each sample and represent less than 15% of the count.

Elements MacGinitie considered as montane elements, such as *Abies* and *Pinus*, from 2-15% and *Picea* plus *Quercus*, represent from 3-10% of the pollen tally at section **W1**; because these taxa are moderate to high pollen producers, their source trees were probably on higher ground some distance from the lake at this time in Florissant history. As Gray (1986) and Spicer (1989) have indicated, the representation in the pollen and leaf records relate strongly to the



proximity of the source plant to the site, as well as to other complex factors such as their productivity of pollen and spores and their habitat.

### **Geographic floral elements and ecological conditions**

MacGinitie's (1953) eight geographic groups and his list of most similar living species (**top of Table 3**) indicated that the primary affinities of the leaf flora are with Group 2, the temperate subhumid Edwards Plateau of central Texas southwards to San Luis Potosi of Northeastern Mexico, and with Group 1, the temperate humid area of southern Colorado to Chihuahua of central northern Mexico (Fig. 6; MacGinitie, 1953, p. 38). His data indicated that an important secondary affinity of the flora is with Group 6, warm-temperate to subtropical taxa of central and southern China, and Group 5, with warm temperate taxa growing in central and eastern USA. Minor relationships are with subtropical Mexico, subhumid scrub taxa of southern Arizona and seasonally dry areas of northern Mexico, and California.

Manchester's review (this volume) indicates that a number of genera, especially 15 taxa of the Ozark Plateau and eastern USA, 8 taxa of Group 6, and 11 taxa of Group 2 were thrown in doubt. Pollen evidence ascertains some of these, and the net effect is that the primary affinities of the Florissant flora are still with Group 2, (Edwards Plateau to Northeastern Mexico), Group 1 (Southern Colorado to Chihuahua), and Group 6 (Central and Eastern China).

By our addition here of 26 new genera or subgenera we add new information, based on affinity with taxa that are limited in their climatic distributions today. We discuss here the biogeographic significance of these (lower part of Table 3). The effect is that the pollen data only strengthen the original affinities cited by MacGinitie, and also our findings add a number of warm temperate to tropical forms.

Group 6. Several newly identified genera (Table 3) now are restricted to summer-moist climates of central and eastern China (*Engelhardtia*, *Eucommia*, *Platycarya*, *Cyclocarya*, *Pterocarya*, ) where they are associated with Mixed Mesophytic forest or mixed deciduous forest; (*Engelhardtia* ranges southward into full tropical forest environments of SE Asia, while *Alfaroa* is subtropical in Central America). Though these genera have only one or a few species existing today (3 are monotypic), their fossil records clearly indicate that they grew in summer-moist, very warm-temperate to subtropical climates during the Eocene (Manchester, 1981; Wing and Hickey, 1984; Leopold and MacGinitie, 1972) Newly discovered taxa such as Rhoipteleaceae (monotypic family of the Mixed Mesophytic forest in China; Wang, 1961) may also represent a moist, warm climate in the past, as it does today. Though we are aware of the danger of extrapolating from monotypic genera whose former tolerances may no longer be typical of the remaining monotypic species, even without these three, the representation of Group

6 is increased from 19 to 25, and with monotypic groups it is increased to 28 (41% of 62 species or taxa whose modern geographic affinities are known).

The fossil *Lygodium kaulfussi* leaves and spores are associated with the warmest interval of the Rocky Mountain Eocene (MacGinitie, 1974). The living genus is a scandent vine mainly of tropical/subtropical distribution. In subtropical and tropical Mexico it grows along the edges of marsh and mangrove vegetation. It probably grew along the edges of the Lake Florissant.

Group 5. *Fagus*, *Ostrya* and *Juglans* have ranges in warm-temperate, summer-moist areas of eastern US, Mexico and eastern Asia, and *Juglans* (black walnut) also has species in low elevation riparian habitats of California, Arizona, Texas, and Mexico (Group 7). *Ostrya* is scattered in montane riparian habitat of Arizona, west Texas, and northeastern Mexico. Palms grow with the oak and pine vegetation in both the occidental and oriental Sierra Madres at 1300-2000m (Martin, 1958). The diversity of evergreen oak taxa is reminiscent of the Sierra Madre Occidental where Paul Martin has seen 10 species of oaks growing at a single site (Basaseachic Falls; Paul Martin, written communication, 1994).

Eight new taxa are added to Group 6, of the central and southern China area with three of these genera also occurring in forests of eastern US (not counting *Juglans*). Hence in terms of geographic elements those groups are now as important as are the temperate humid plants of Group 1 (southern Rocky Mountains south to Chihuahua) and Group 2 (Edwards Plateau of Texas south to San Luis Potosi). Our expansion of Group 6, because of their summer moisture requirements, enriches the streamside/lakeside vegetation described by MacGinitie, and adds several taxa that are now chiefly subtropical (*Lygodium*, *Engelhardtia*, and *Cyclocarya*). While one *Lygodium* species ranges into warm temperate areas (e.g. *L. palmatum*), the spore type represented here is most like the Eocene Wyoming species, *L. kaulfussi*, which is associated with subtropical vegetation. *Engelhardtia* species that occur in the the Mixed Mesophytic forest of China have very small pollen (*E. colebrookiana* for example), but the large *Engelhardtia* pollen type here is like *E. spicata*, a tropical species. It does also resemble the large juglandaceous pollen of *Alfaroa* of Central America. Based on the affinities with present species or on their fossil occurrence these represent three subtropical elements; they expand MacGinitie's list of about 9 subtropical-tropical taxa at Florissant. These pollen types are regular participants in the Green River and in the Kisinger Lake (middle Eocene) floras of Wyoming.

In Group 4 of MacGinitie we add three taxa that are members of the subhumid scrub flora (southern Arizona to Sinaloa). *Sarcobatus*, or greasewood is a shrub that inhabits brackish or saline valley bottoms. *Datura* cf. *D. discolor* is now found in warm desert scrub areas, and in Group 7, *Xylomera* and *Semeiandra* are woody evening primroses that live in warm disturbed environments of northern Mexico. These may have occupied lowland areas around Lake Florissant.

In Group 1 is *Elaeagnus* cf. *E. argentea* (buffalo berry), a shrub now common at low elevations in the Rocky Mountains. This genus also has a long fossil record in the Eocene of that region. *Ephedra* cf. *E. torreyana* likewise has a long Tertiary record in the western USA. In Group 7, *Abies* occurs as low as **1300 m** in the Cloud Forest of Northeastern Mexico (Martin, 1958).

### **Climatic conditions estimated from the flora.**

Based on the composition of the flora and the climate characteristics of the present living relatives, MacGinitie estimated the character of the Florissant climate as follows: mean annual temperature of "not less than 18° C (65°F)" with an absolute minimum temperature of "probably not below -7°C (20°F), and the mean summer temperature of about 26-27°C (80°F)". Rainfall would have been confined to the warm season, mostly in late spring and early summer, and was not adequate to support "true" forest except along streams and lakes. Similar climates are found in the northern Sierra Madre of northeastern Mexico between latitudes 20° and 30° (see Fig. 6; Appendix).

A mean annual "biotemperature" of ~18°C is cited by Holdridge (1967) in his vegetation classification of latitudinal regions which marks the boundary between subtropical and warm temperate regions. For example, a mean biotemperature of between 18-24°C comprises subtropical vegetation while between 12 to 18°C is considered warm temperate. "Biotemperature" of Holdridge is the average monthly temperatures for all months above freezing, divided by 12; so for a climate like that of the Edwards Plateau (Table 3) or mid-montane Tamaulipas, the biotemperature is the same as the MAT.

Our additions to the Florissant flora fit well with MacGinitie's MAT determination of ca. 18°C, as our data reinforce the importance of subtropical to tropical elements, e.g., the addition of *Cyclocarya*, *Engelhardtia*/*Alfaroa*, *Lygodium*. Further we have added these warm temperate taxa: *Carya*, *Eucommia*, *Fagus*, *Platycarya*, *Rhoipteleaceae*. The additions fit into MacGinitie's ecological groups of plants, but several taxa range beyond his groupings; for example, in the southern part of its range, *Sarcobatus* in its distribution in warm deserts of central Arizona at 300 m, defines a subtropical lower montane desert scrub zone. *Datura* and *Xylomera* probably represented the same type of vegetation. *Sarcobatus* today ranges northward to the Utah border in warm temperate saline lowlands, and was common throughout the Eocene of the Rocky Mountain region.

Though the Florissant assemblage differs from the Bridgerian Green-River flora (late middle Eocene age; MacGinitie, 1969) of Wyoming and Colorado, there are a striking number of forms in common. These include: *Lygodium*, Pinaceae (*Abies*, *Picea*, *Tsuga*, *Pinus*), *Ephedra*, *Sequoia*-type, *Sarcobatus*, *Typha*, palm types, Poaceae, *Castanea*/*Castanea*, *Quercus*,

*Ulmus/Zelkova*, *Carya*, *Pterocarya*, *Cyclocarya*, *Platanoidites*, *Platycarya*, *Engelhardtia/Alfaroa*, *Ostrya/Carpinus*, *Eucommia*, *Morus*, *Salix*, *Croton*, *Dodonea*, *Elaeagnus*, Rosaceae types, *Astronium* -type, Sterculiaceae/Fremontodendronae, Sapindaceae cf. *Cupanea* (Robert Cushman, in preparation; Leopold data). The leaf data indicate a strong tropical aspect to the Green River flora and a subtropical to warm temperate aspect for the Florissant flora. The pollen data showing a number of the warm temperate to tropical elements occurring at both floras support this conclusion.

**Figure 6      Map of Mexico and SW USA      Near Here**

**Paleoaltitude of the Florissant Basin in the context of climate**

MacGinitie used floristics to estimate paleoclimatic conditions. From the biogeographic affinities of his about 100 identified Florissant species and taking note of his several (at least 9) subtropical elements, he arrived at a MAT not lower than 18°C. MacGinitie also estimated the general paleoelevation of the Florissant Basin to be below 1000 m, based on the geographic occurrence today of assemblages with affinities to the Florissant flora.

Gregory and Chase (1992) and Wolfe (1992) made paleotemperature estimates of the Florissant assemblage based on the CLAMP method of Wolfe (1991, 1992). This interesting method utilizes the architecture of leaves (the presence or absence of serrate teeth, drip points, and leaf size, to name a few features) to correlate with local climate stations, and uses these as a predictor of paleoclimate. The CLAMP method may ultimately provide an accurate estimate of MAT independent of taxonomic identifications or affinities of the flora. Wolfe has developed a database for many stations within the USA and Asia for this purpose, but as yet has not provided similar information from Texas or Mexico. Using CLAMP the paleotemperature estimates for the Florissant basin by Gregory and Chase (1992) using 29 species of fossil leaves was 10.7°C and using 97 species was 11.6°C MAT. Wolfe's (1992) estimate using CLAMP was 12°C.

The determination of fairly low MAT temperatures for Florissant fossil beds using the CLAMP method effects the compositional nature of the flora. By necessity the range of average monthly temperatures at Florissant has to be low in order for the climate to have had only light frosts. A paleotemperature of only 11.6°C or even 10.7°C, under Holdridge's system would represent a cool temperate climate for most areas of the USA, except on the west coast; (Cape Blanco on the coast of Oregon for example is a cool-temperate area with a relatively frost-free winter with a MAT of 10.3°C). Exceptions would be special areas such as Holdridge's Tropical Montane Rainforest (MAT 11°C) or Christchurch, New Zealand. In general a cool temperate climate with frosty winters would be incompatible with subtropical and warm temperate taxa, and would put subtropical species under considerable stress. While it is clear from the plant

affinities that the Florissant climate was temperate, it was warm temperate, not cool temperate, as might be implied by an estimated MAT of 10.7°C. Hence we have real concerns regarding the relatively cool temperatures now proposed by CLAMP, particularly in view of the present lack of a Mexican and Texas database for the areas thought to represent the general counterparts for the paleoflora.

Another tool developed by Wolfe (1993), Meyer (1992; this volume) and used by Gregory and Chase (1992) involves estimating vertical lapse rates (change of temperature with altitude) in order to calculate paleoaltitudes for fossil floras of Tertiary age. The modern lapse rate for central Colorado which is shown in **Figure 7a**, has a slope of 5.89°C per km. If we use the present regional lapse rate to plot the various CLAMP temperature estimates (Fig. 7a) to estimate paleoelevation, we see that these points would fall below 1400 m; for example, a MAT of 10.7 would represent an elevation of ca. 1400 m; and a MAT of 12°C would be at about 1200 m. MacGinitie's estimate of 18°C would fall at only about 900 m (**Fig. 7a, b**). In keeping with such estimates, for example in Northeastern Mexico (Taumaulipas highlands), frosts occur 20-50 days of the year above an altitude of 1800 m.

In contrast, Wolfe (1992a) pointed out that the past lapse rates may have been different from today's. He calculated the Eocene lapse rate to have a slope of 3.06°C/km (**Fig. 7b**), or about 3°C based on lapse rates along the California coast. The sea-level MAT at latitude from along the Pacific coast with the base of his line near sea level is set at 21-23°C based on his estimated paleotemperatures from the late Eocene Laporte, Potbury and Goshen floras. From this curve Wolfe obtained his relatively high estimate of paleoaltitude of 2700-2900 m for Florissant. Gregory and Chase (1992) who also used a Pacific coast lapse rate of 3.2° and 2.3° C/km estimated elevation to be a bit lower (2400-2700 m). Meyer (1986, this volume) using a highly local lapse rate for the western slope of the Front Range estimated 2450 m. These paleoaltitudes would place Florissant either near its present elevation of 2500 m, or up to 400 m higher, which is near the present altitudinal limit of trees on Pikes Peak.

It is clear that these calculations and reasoning depend chiefly on which lapse rate is used. Given our limited knowledge about late Eocene ocean temperature and upwelling along the west coast, coastal temperature, and meridional circulation that effect this parameter, it seems premature to make a firm judgement about lapse rates in the Eocene. Doubtless the lapse rate was lower, but we may know so little compared to what we need to know about Eocene conditions that such estimates may be very shaky.

There are many variables (only one of which is lapse rate) that may have been different in the past. Another variable according to MacGinitie (1969, p. 46) is the fact that "both the Green River and Florissant floras contain species whose living correlatives are adapted to subhumid and/or seasonally dry habitats. This element is lacking or extremely rare in the west coast floras".

....."It is clear that we cannot use data based on the leaf characters of living or fossil lowland floras in interpreting the climatic environments of the central Rockies for any flora which postdates the Wasatchian orogeny. We are dealing with entirely different floral assemblages." Based on MacGinitie's concerns it may be difficult to estimate quantitatively the altitude of these late Eocene basins using the flora itself. In any case, geologic evidence will be of critical importance, and whether or not the Florissant basin either has been lifted considerably after the Eocene (Trimble, 1989) or dropped in elevation since deposition ( \_\_\_\_\_, **this volume**) must be considered.

## CONCLUSIONS

The information gleaned from pollen and spores at the Florissant fossil beds has provided a number of new taxa and ecological information about the paleoenvironment and flora. These findings especially add to the lakeside and riparian group of plants that probably represented deciduous forest around Lake Florissant. Eight of these have their modern relatives in the warm temperate zone of central and southern China. Four trees are closely related to eastern US taxa and to Ozark Plateau species, and because these also require summer moisture, were probably growing in riparian low areas of the basin. Subarid shrubs such as greasewood and a woody evening primrose add to MacGinitie's group of scrub taxa that suggest dry or even saline environments. The montane elements are members of the pine family and oak that fit well with the macrofossil evidence of upland vegetation, such as MacGinitie has described from the slopes of the Tamaulipas highlands in northeastern Mexico.

The pollen evidence in several instances corroborates the subgeneric affinities of megafossils cited by MacGinitie. One of the outstanding examples is the huge pollen resembling *Abies venusta*, an endemic species of fir in the Santa Lucia Mountains of California. The seeds resembling this species were identified as *A.venusta* type by MacGinitie.

Most importantly, the warm character of the pollen flora substantiates the diagnosis provided by MacGinitie's macrofossils. Three subtropical types and about 10 warm-temperate woody genera are added to the flora. Using the character of the flora as climate indicator, our microfossils fit well with an estimated MAT of 18°C. Estimates of Eocene paleotemperature at Florissant using CLAMP methods will be more appropriate after modern climate and vegetation data from the nearest modern counterpart vegetation (e.g. Texas and northeastern Mexico) are included in the baseline database.

Though the temperature estimates based on the CLAMP (leaf physiognomy; multiple regression) model seem more cool-temperate than the flora warrants, if we plot these on a modern mean lapse rate for central Colorado, it suggests that the altitude of Florissant was below 1400 m in elevation at the time of deposition. MacGinitie had estimated the elevation as

no higher than about 900 m (or 3000 ft). The use of lower lapse rates suggests a much higher altitude for the site similar to the present elevation of 2500 m or even higher. It may be premature to estimate altitudes quantitatively in midcontinent areas using lapse rates, since there is much that is not yet known about the factors that effected climatic gradients and about contrasts between coastal and mid continent conditions during the Paleogene.

#### **ACKNOWLEDGEMENTS**

We appreciate the helpful comments of Paul Martin and Steve Manchester and Howard Schorn on our manuscript. William Bradley was an inspiration for writing this approach to the pollen work.

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